

Effects of longitudinal and lateral stream channel complexity on native and non-native fishes in an invaded desert stream

NATHAN R. FRANSSSEN*, ELIZA I. GILBERT† AND DAVID L. PROPST*

*Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM, U.S.A.

†New Mexico Department of Game and Fish, Fisheries Management Division, Santa Fe, NM, U.S.A.

SUMMARY

1. Understanding how habitat heterogeneity influences the structure of communities has been a longstanding goal of ecologists. Identifying how stream channel complexity affects fishes will be particularly important in systems simplified by anthropogenic activities and encroachment of non-native riparian vegetation.
2. Here, we assessed how large-scale longitudinal distribution of lateral stream channel complexity from anthropogenically channelised, naturally braided and canyon-bound reaches of the San Juan River in New Mexico and Utah, U.S.A., correlated with species richness, evenness and the relative abundance of small-bodied native and non-native fishes. We also contrasted fish assemblages at a smaller scale, in the most laterally complex reach of the river, by comparing fish assemblages between primary channel and secondary channel habitats as well as in newly restored secondary channels.
3. Rarefied fish species richness was generally highest in the braided reach of the river and the longitudinal distribution of total fish densities varied temporally. Contrary to our predictions, native fish densities were highest in the most upstream and anthropogenically channelised reach of the river. Non-native fish densities tended to be highest in the downstream braided reach, and all fishes were sparse in the least complex canyon-bound reach. Total fish densities were higher in secondary channels compared with primary channels, and non-native fishes were responsible for this difference. Fish assemblages in recently restored secondary channels were generally similar to those in naturally occurring ones.
4. Our results suggest that lateral channel complexity can facilitate greater species richness at larger scales and is likely to provide habitats for fishes that are rare or not found in larger primary channels. These findings also suggest reduced channel complexity may lower the ability of riverine systems to support diverse fish assemblages.

Keywords: channel braiding, channel simplification, habitat complexity, invasive species, stream restoration

Introduction

Habitat structure can play a pivotal role in regulating local species diversity with more physically complex habitats usually supporting greater numbers of species (Bell, McCoy & Mushinsky, 1991). The relative and absolute abundance of different structures in habitats are thought to mediate the mechanistic relationship between habitat complexity and biodiversity (Bell *et al.*, 1991).

Thus, understanding how habitat heterogeneity influences biodiversity will require identifying habitat structures relevant to the species of interest while acknowledging that other environmental filters may limit the presence of species (Poff, 1997; Jackson, Peres-Neto & Olden, 2001).

Environmental conditions such as discharge patterns, temperature regimes and the geomorphology of river basins can drive spatial and temporal variation in abiotic

components of riverine ecosystems (Petts, 1994). Much environmental variation can occur predictably along stream courses, shaping the degree of stream channel complexity (Thorp, Thoms & Delong, 2006) and longitudinal composition of faunal communities (Vannote *et al.* 1980). The structure of fish assemblages typically transitions from one or a few headwater specialist species to a diversity of forms and life history strategies in large, mainstem systems (Rahel & Hubert, 1991). Therefore, the composition of local assemblages will be dictated by the ability of resident species to withstand or exploit local environmental conditions and degrees of habitat complexity that can be variable over time and across multiple spatial scales.

Although introduced fishes can persist in invaded systems, their specific ecologies limit their relative success and longitudinal distributions within catchments. Explanations for non-native fish invasion and persistence range from introduced species being able to exploit unutilised or under-utilised resources (Moyle & Light, 1996a; Gido & Brown, 1999; Gido & Franssen, 2007), out-compete natives (Douglas, Marsh & Minckley, 1994; Rahel, 2002) or flourish after release from their native parasites (Torchin *et al.*, 2003). Several studies of invaded streams in California, U.S.A., indicated that while biotic interactions influenced spatial distributions of native and non-native fishes, longitudinal environmental gradients were also important factors (Moyle & Light, 1996b; Marchetti & Moyle, 2001; Moyle & Marchetti, 2006).

After large-scale environmental gradients filter the available species pool, smaller-scale habitat conditions can dictate the structure of local fish assemblages. Positive relationships between habitat complexity and species diversity suggest local habitat heterogeneity can facilitate the coexistence of species (Huston, 1994; Rosenzweig, 1995; Stein, Gerstner & Kreft, 2014). Similarly, stream habitat variation over different spatial scales can have strong influences on the diversity of freshwater fish assemblages (Gorman & Karr, 1978; Schlosser, 1987; Pearsons, Li & Lamberti, 1992), and correlations between habitat complexity and fish species diversity and abundance have been noted in a variety of aquatic systems (Angermeier & Schlosser, 1989; Horan *et al.*, 2000; Ferreira, Goncalves & Coutinho, 2001; Gratwick & Speight, 2005; Muotka & Syrjanen, 2007). However, little is known about how habitat heterogeneity interacts among various spatial scales to influence the structure of fish assemblages (Fausch *et al.*, 2002).

Lateral stream complexity (i.e. channel braiding) can provide hotspots of biodiversity, presumably as a result

of variable habitat structure (Buijse *et al.*, 2002; Arscott, Tockner & Ward, 2005; Gray, Scarsbrook & Harding, 2006; Karaus *et al.*, 2013). Secondary channels created by river braiding may also serve as refuges for fish during floods (Junk, Bayley & Sparks, 1989; Pearsons *et al.*, 1992; Lake, 2000; Buijse *et al.*, 2002) and create connections to low-velocity and floodplain habitats used for spawning and growth of larvae and juveniles (Junk & Welcomme, 1990; Bayley, 1995; Welcomme, 1995). Across the planet, stream channel simplification from urbanisation (Bernhardt & Palmer, 2007), encroachment of invasive riparian vegetation (Tickner *et al.*, 2001) and confinement of natural channel migration are major threats to aquatic biodiversity (Dudgeon *et al.*, 2006). Understanding how native and non-native fishes respond to stream channel complexity, especially in the context of longitudinal environmental gradients, will be paramount for ameliorating effects of stream habitat homogenisation. Furthermore, such knowledge may inform current approaches used to enhance native fishes and mitigate potential negative effects of invasive species.

The San Juan River, a major tributary of the Colorado River, U.S.A., demonstrates considerable longitudinal and lateral habitat heterogeneity and harbours several non-native fishes. The river was impounded in 1962, fragmenting and truncating stream habitats as well as modifying the river's natural flow regime (Franssen, Gido & Propst, 2007). But longitudinal gradients still persist with increased temperature and lower primary and secondary productivity moving downstream (Bliesner & Lamarra, 2000). In addition to changes wrought by impoundment, local straightening of the main channel and encroachment of invasive salt cedar (*Tamarix* spp) and Russian olive (*Elaeagnus angustifolia*) (Birken & Cooper, 2006; Nagler *et al.*, 2011) have altered the heterogeneity of the river's channel. Most anthropogenically driven river channel confinement has occurred in upper reaches, while non-native vegetation encroachment has occurred in the floodplain river wide. Resource agencies have recently restored several secondary channels in the San Juan River to improve channel braiding for federally protected fishes in the system, namely Colorado pikeminnow (*Ptychocheilus lucius*) and razorback sucker (*Xyrauchen texanus*). Portions of the river are also naturally confined by geological formations; in lower reaches of the river, a deep canyon restricts lateral channel migration. Thus, the San Juan River demonstrates natural and unnatural longitudinal variation in channel complexity. Upstream reaches are affected by anthropogenic channelisation, middle reaches contain the greatest

levels of channel braiding, and lower reaches contain mostly a single channel.

Considering the extensive and expensive efforts to restore habitat complexity to benefit native biota in stream systems (Bernhardt, Palmer & Allan, 2005; Palmer, Menninger & Bernhardt, 2010), understanding how stream channel complexity will affect both native and non-native species is of critical importance in river restoration (Newson & Large, 2006). Here, we test the hypothesis that longitudinal and lateral channel complexity predictably affects the structure of fish assemblages. Specifically, we predicted channel braiding at the reach scale would increase the richness, evenness and abundance of both native and non-native fishes. At a smaller scale, we predicted secondary channel habitats would have higher species richness and abundance of non-native fishes compared with primary channels.

Methods

Study area

The San Juan River originates in the San Juan Mountains of southwest Colorado and flows nearly 484 km west through New Mexico and Utah before its confluence with the Colorado River at Lake Powell (Fig. 1). Closure of the Navajo Dam truncated upper portions of the river and completion of Glen Canyon Dam, filling Lake Powell in the 1980s, inundated lower reaches of the river, leaving 365 km of contiguous, free-flowing stream habitat.

The San Juan River's stream channel is longitudinally and laterally heterogeneous between Navajo Dam and Lake Powell (Bliesner & Lamarra, 2000). The variable channel morphology, in large part, results from

interactions among the river's underlying geology, variation in floodplain width, high gradient and considerable intra- and inter-annual flow variation (Bliesner & Lamarra, 2000; Propst & Gido, 2004). These natural factors, as well as human modifications, created a stream system that has three relatively distinct reaches that can be demarcated by the longitudinal frequency of channel braids (i.e. secondary channels, Fig. 2). Lowermost San Juan River is a single canyon-bound channel (canyon reach), while the middle portion is in a broad floodplain with multiple secondary channels (braided reach, Bliesner & Lamarra, 2000). The uppermost San Juan River is somewhat constrained by anthropogenic activities (e.g. artificial bank protection) and consists primarily of a single channel (channelised reach) with considerably fewer secondary channels than the middle reach. Most secondary channels are relatively permanent features with vegetated islands separating them from the main channel, but discharge dictates their temporal connectivity to the primary channel.

While many secondary channels have flowing water at base discharge, sediment deposition has closed mouths of some and thus dried or reduced them to disconnected pools of standing water. To increase channel complexity, six historical secondary channels were reconnected in 2011 by removing sediment that hindered inflow from the primary channel (Keller-Bliesner Engineering, 2012). The project restored 5.6 km of secondary channel habitat and cleared 2.6 ha of non-native riparian vegetation.

Fish sampling

We collected small-bodied fishes each autumn from 1999 to 2012 from wadeable habitats with seines

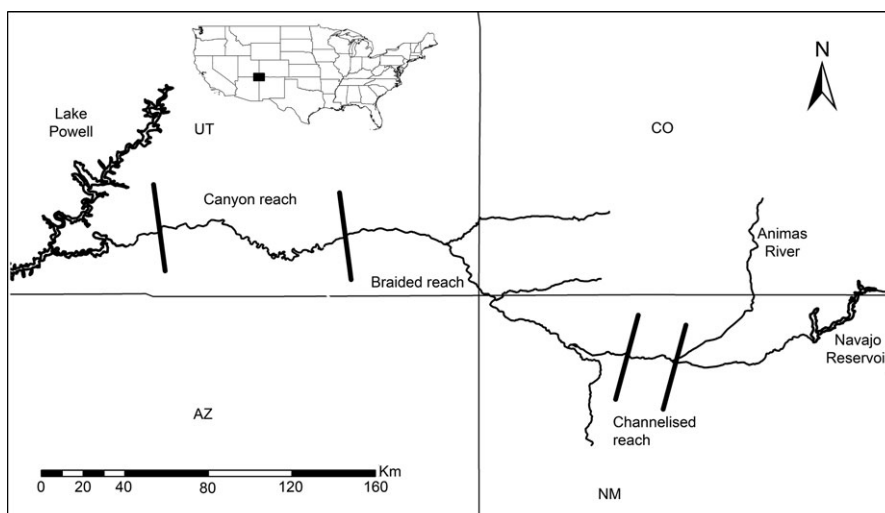


Fig. 1 Study area on the San Juan River, New Mexico and Utah, U.S.A. The three separate reaches were demarcated by high levels of anthropogenic channel straightening (channelised reach), high frequencies of natural secondary channels (braided reach) and a naturally confined stream channel (canyon reach).

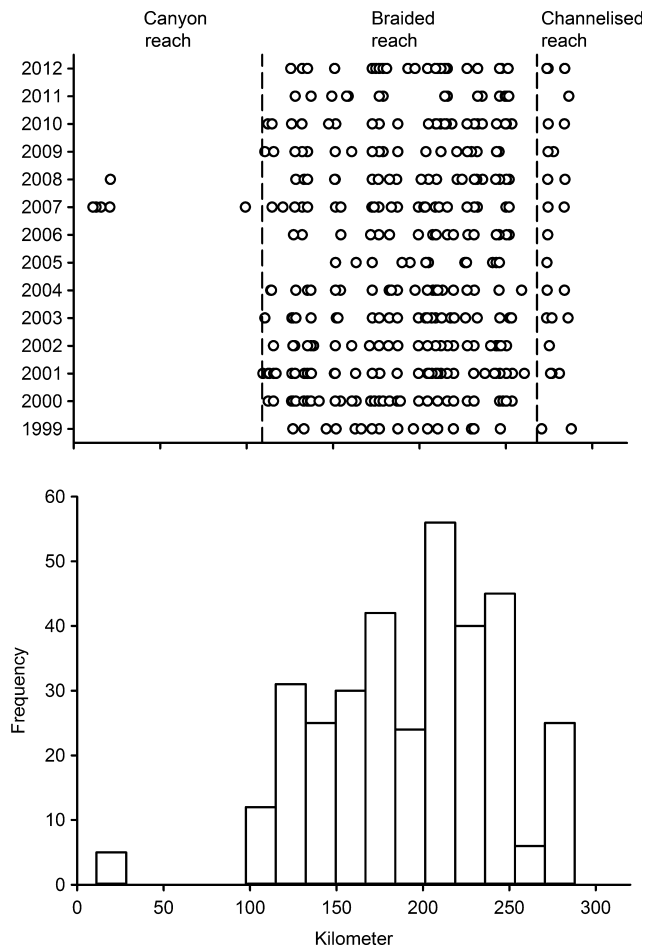


Fig. 2 Locations of all sampled secondary channels over time by river reach (top panel) and the frequency of secondary channels by river kilometre over the entire study period (bottom panel).

(2.2 m × 1.9 m, 3.2 mm mesh) in both primary and secondary channels in our predefined reaches (Fig. 1). Sample sites were accessed by raft, and the primary channel was sampled every fifth river kilometre from the confluence of the Animas River to just above Lake Powell. In 2011 and 2012, sampling did not occur in the canyon reach, and in 2000, the channelised reach was not sampled. Secondary channels, in our study, were defined as branches of the primary channel with 25% or less of total discharge (visually estimated) at the time of sampling and at least 200 m in length. To the extent possible, all secondary channels with flowing water were sampled each year. However, annual variation in channel morphology and sediment elevations dictated the flow in secondary channels, and thus, not every secondary channel was sampled every year. We sampled about 100 m at each site, and mesohabitats were sampled in rough proportion to their availability. Maximum depths of sampled habitats ranged from 10 cm or less in

shallow runs and riffles to 2 m in pools and runs. Substrata were cobble and gravel in riffles, gravel and sand in runs, and sand and silt in pools and backwaters (Propst & Gido, 2004). The entire breadth of secondary channels was usually sampled, but most primary channel sampling was shoreline (typically within 10 m). We sampled three of the six restored secondary channels in 2012 (1 year after restoration).

Captured fishes were identified to species and counted; native fishes were returned to the river (except that individuals too small to accurately identify in the field were fixed in 10% formalin and returned to the laboratory for identification). We quantified the area of each seine haul by multiplying seine haul length and width, and calculated fish density as the total number of fish captured per total area sampled (i.e. fish m⁻²) at each site.

Data analysis

We were interested in assessing the influence of secondary channels on fishes at two spatial scales. The first was large-scale variation among our predefined river reaches, and the second was at a smaller scale focusing on fishes in secondary versus primary channels in the braided reach. We limited channel-scale analyses to collections where primary channel sites were within 1.6 river km of secondary channel sites to help control for longitudinal variation in fishes within the braided reach (i.e. we had paired primary and secondary channel sites in each year; Table 1).

Species richness, assemblage evenness and fish densities

We assessed variation in species richness and evenness among reaches (large scale) and between channel types (small scale). Because some collections contained very few individuals (e.g. 1), we aggregated collections by reach or channel type each year before we estimated richness and evenness. We estimated species richness among reaches and between channel types with rarefaction (Gotelli & Colwell, 2001) by randomly resampling 124 individuals without replacement from reaches and 243 individuals from channels (i.e. the smallest sample sizes in reaches and channels) over 999 iterations in each year. We quantified evenness among reaches and between channel types following Pielou (1969): $J = H' / \ln(S)$, where H' is the Shannon diversity index and S is species richness. All fish were included in species richness and evenness estimates, but only fish species that occurred in at least 5% of collections were

Table 1 Number of collections per year by reach and channel type. Blank cells represent no collections. Data from 2000 were not included in the reach-scale analyses but are presented here for completeness

Year	Channelised	Reach Scale		Channel Scale	
		Braided	Canyon	Primary	Secondary
1999	4	30	20	11	11
2000		32	22	19	19
2001	9	35	24	18	18
2002	6	32	22	15	15
2003	7	33	20	11	11
2004	9	38	21	13	13
2005	8	35	20	6	6
2006	5	35	19	13	13
2007	9	50	22	16	16
2008	8	34	11	11	11
2009	8	32	24	12	12
2010	7	34	22	14	14
2011	7	26		5	5
2012	9	30		13	13

included in further statistical analyses. Prior to analyses, we $\log_{10}(X + 0.001)$ -transformed fish densities to approximate normality of residuals and to reduce the influence of super-abundant species.

We tested for variation in species richness, evenness and densities of total, native and non-native fishes among reaches and between channel types with linear mixed models (LMM) using the nlme package (Pinheiro & Bates, 2000) and linear models in the R statistical language (R Development Core Team, 2011). Each model contained a fish assemblage metric as the dependent variable with Reach (or Channel) as a fixed effect and Year as a random effect (when possible). The significance ($\alpha = 0.05$) of random effect interactions of Reach (or Channel) \times Year for each LMM was assessed by the likelihood ratio test comparing the full versus reduced models using the maximum-likelihood estimator (Pinheiro & Bates, 2000). Interactions were only included in final models if significant. Because we aggregated fish collections within reaches and channel types each year to quantify species richness and evenness, the term Year could not be included in the channel-scale models due to the lack of at least three replicates in each year (as well as in the reduced reach-scale analysis, see next paragraph). Estimates and tests of significance of the final LMMs were quantified using the restricted maximum-likelihood estimator (Pinheiro & Bates, 2000).

At the reach scale, an unbalanced design prevented statistical analyses of the data set in its entirety (i.e. the channelised reach was not sampled in 2000, and the

canyon reach was not sampled in 2011 and 2012; see Methods above). Therefore, to maximise power of analyses and to meet the requirement of balance among factors, we removed some data and partitioned the remaining data set. Because 2000 was the only year missing data from the channelised reach, all data from this year were removed from the reach-scale analyses. We then analysed the remaining data in two subsets. The first subset included data from 1999 to 2010 using all reaches, and the second included all years but only the channelised and braided reaches. Thus, the first set allowed us to assess variation among all reaches with limited annual replication, while the second set allowed for comparisons between the channelised and braided reaches maximising the number of years in the analysis. Because the second set of data only included two reaches in the analyses of richness and evenness, the random effect of Year could not be included in these models (there were only two data points per year).

Restored secondary channels

We quantified the same fish assemblage metrics described above in collections from the three restored secondary channels in 2012 (1 year after restoration). Because of the relatively small number of individuals collected in the restored secondary channels, we calculated mean richness among the three channels rather than rarefying species richness. Metrics of fish assemblage structure in secondary channels were then qualitatively compared to assemblages in the primary and secondary channels of the braided reach.

Fish assemblage variation

To summarise variation among collections, we used principal components analyses (PCA) using correlation matrices of standardised fish densities. A PCA was performed on the reach- and channel-scale data separately. Only axes with eigenvalues >1.0 were retained for interpretation, and variation in axis scores was characterised among years and reaches (or channel types).

We identified species that contributed to the spatial variation in fish assemblages with indicator species analyses (Dufrêne & Legendre, 1997) using the indval function in the labdsv package in R. Reach (or channel type) was entered as the predefined clusters with all years of data combined, and we used 9999 permutations to assess significance of each species in each cluster (we only report significant species/cluster associations at $\alpha = 0.05$).

Results

Nineteen fish species were collected between 1999 and 2012, but only seven were native to the San Juan River (Table 2). Speckled dace (*Rhinichthys osculus*) was the most frequently encountered native species followed by flannelmouth sucker (*Catostomus latipinnis*) and bluehead sucker (*C. discobolus*). Native mottled sculpin (*Cottus bairdii*) and roundtail chub (*Gila robusta*) were extremely rare. *Ptychocheilus lucius* were present mainly as stocked individuals, and we did not collect any *X. texanus*

Table 2 Percentage of fish species in all collections between 1999 through 2012 on the San Juan River by reach and between channel types in the braided reach. Non-native fishes are denoted by an asterisk

Species	Reach			
	Channelised	Braided		Canyon
		Primary	Secondary	
<i>Rhinichthys osculus</i>	97.1	91.8	89.0	51.4
<i>Catostomus latipinnis</i>	76.7	55.3	51.9	18.2
<i>Catostomus discobolus</i>	78.6	36.8	33.1	12.1
<i>Ptychocheilus lucius</i>	2.9	16.8	12.7	3.2
<i>Cottus bairdii</i>	1.0	0	0	0
<i>Gila robusta</i>	0	0.4	0.6	0
<i>Cyprinella lutrensis</i> *	12.6	81.1	89.0	76.9
<i>Ictalurus punctatus</i> *	0	51.9	48.1	70.0
<i>Pimephales promelas</i> *	48.5	37.0	51.4	15.8
<i>Gambusia affinis</i> *	16.5	20.2	33.7	8.5
<i>Fundulus zebrinus</i> *	14.6	7.1	9.9	1.2
<i>Cyprinus carpio</i> *	3.9	5.0	15.5	2.8
<i>Micropterus salmoides</i> *	9.7	1.9	2.2	0.4
<i>Lepomis cyanellus</i> *	7.8	1.3	0	1.2
<i>Ameiurus melas</i> *	1.9	1.5	0.6	0.8
<i>Salmo trutta</i> *	3.9	0.2	0	0
<i>Oncorhynchus mykiss</i> *	1.9	0	0	0
<i>Ameiurus natalis</i> *	1.0	0.8	0	0
<i>Lepomis macrochirus</i> *	0	0.2	0	0

Table 3 Results from linear models and linear mixed models testing for differences in rarefied species richness and evenness (Pielou's J) among reaches and between primary and secondary channels. Interaction terms were not included due to lack of replication in reaches and channels each year

Analysis	Dependent	Fixed effect	d.f.	F	P	Random effect	% Variance
Reach*	Richness	Reach	2,20	2.75	0.088	Year	1.0
	Evenness	Reach	2,20	0.05	0.953	Year	0.01
Reach†	Richness	Reach	1,24	6.61	0.017		
	Evenness	Reach	1,24	0.54	0.468		
Channel	Richness	Channel	1,26	2.74	0.110		
	Evenness	Channel	1,26	0.28	0.604		

*Models exclude 2011 and 2012 data, but includes all reaches.

†Models exclude the canyon reach from all years, tests for differences between the channelised and braided reaches.

specimens. The most frequently collected non-native fishes were red shiner (*Cyprinella lutrensis*), channel catfish (*Ictalurus punctatus*), fathead minnow (*Pimephales promelas*), western mosquitofish (*Gambusia affinis*), plains killifish (*Fundulus zebrinus*) and common carp (*Cyprinus carpio*). The remaining non-native fishes were found infrequently and usually in only one or two collections during the study.

Species richness and evenness

Reach scale. Using the first subset of data (i.e. 2011 and 2012 removed), estimated species richness was not significantly different among reaches (the braided reach tended to have higher richness, albeit not significantly at $\alpha = 0.05$) and Year explained little variation (Table 3; Fig. 3). Evenness was not significantly different among reaches. The second subset of data (all years but only channelised and braided reaches) revealed species richness was indeed significantly higher in the braided reach compared with the channelised reach, and evenness was not significantly different between reaches.

Channel scale. Species richness did not vary between channel types (Table 3), and the range of estimates was relatively small over time (Fig. 4). Evenness also did not differ between primary and secondary channels, but did experience substantial variation temporally, with a general positive trend over time (Fig. 4).

Native and non-native fish densities

Reach scale. Using the first subset of data, total fish densities varied among reaches and the Year \times Reach term was significant (Table 4), indicating total fish densities varied among reaches over time. Total fish densities were generally highest in the braided reach, but only during the first half of the study. In later years,

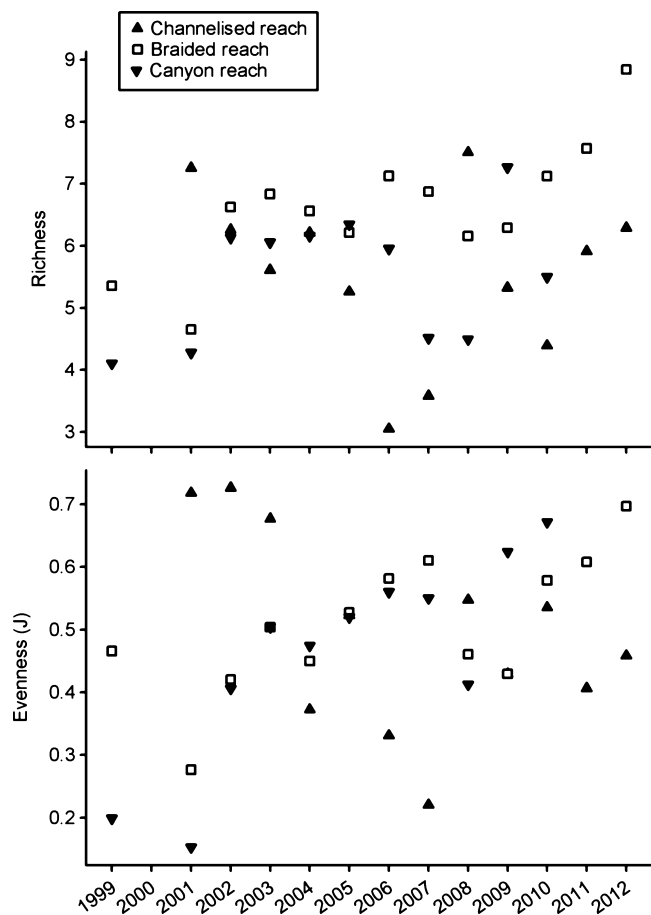


Fig. 3 Mean rarefied species richness (top panel) and species evenness (bottom panel) among river reaches.

the highest total fish densities occurred in the channelised reach followed by the braided and canyon reaches (Fig. 5). Reach had significant effects on both native and non-native fish densities, and the Year \times Reach interactions were also significant. However, these interactions explained relatively little variation. Native fishes showed strong longitudinal patterns in their densities (decreasing from upstream to downstream) and did not show much temporal variation. Densities of non-native fishes tended to be highest in the braided reach followed by the channelised and canyon reaches and generally decreased over time.

Tests of the second subset of data (included all years but only the channelised and braided reaches) revealed both similar and contrasting patterns (Table 4). Here, total fish densities did not differ between the channelised and braided reach, but the Year \times Reach term was significant and explained a considerable portion of the variation. Densities of native fishes varied between

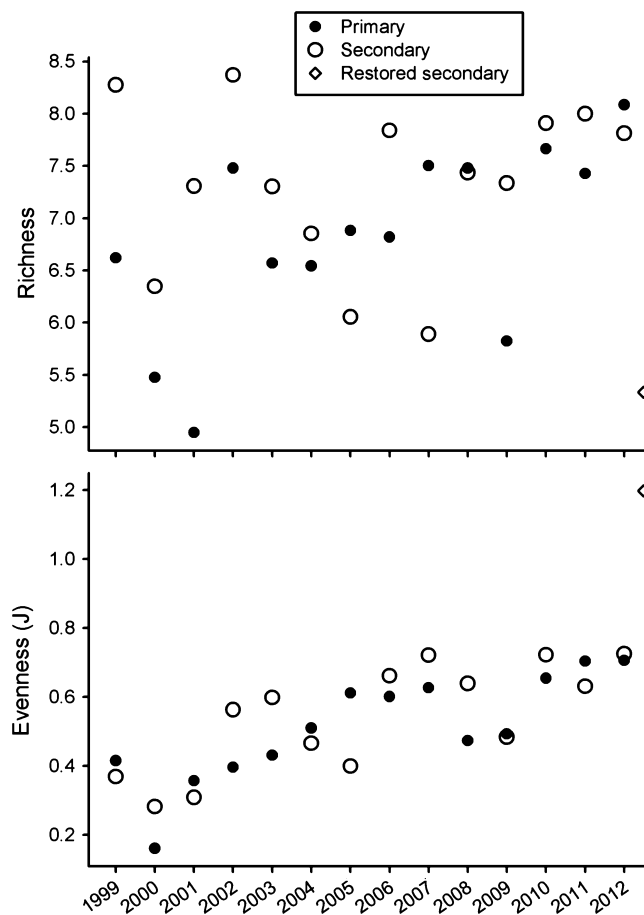


Fig. 4 Mean rarefied species richness between channel types (top panel) and species evenness between channel types (bottom panel) as well as mean observed species richness and evenness in the restored secondary channels in 2012.

reaches with Year \times Reach explaining a significant but small quantity of the variation. Non-native fish densities also varied between reaches, with higher densities in the braided reach compared with the channelised reach (the Year \times Reach was marginally non-significant [$P = 0.052$] and thus not included in the final model).

Channel scale. Total and non-native fish densities varied between channel types (Table 4), and both of these densities were usually higher in secondary channels compared with the primary channel (Fig. 6). Additionally, the Year term explained nearly half of the variation in both cases. Similar to the reach-scale analysis that only included primary channel collections, the channel-scale assessment also demonstrated a general decline in non-native fishes over time. In contrast, native fish densities did not differ between channel types and showed little temporal variation.

Table 4 Results from linear mixed models testing for differences in total, native and non-native fish densities in the primary and secondary channels. Interaction terms were only included in the final models if significant

Analysis	Dependent	Fixed effect	d.f.	F	P	Random effect	% Variance
Reach*	Total	Reach	2,20	15.24	<0.001	Year	11.6
						Year × Reach	23.7
	Native	Reach	2,20	116.59	<0.001	Year	5.7
						Year × Reach	7.4
	Non-native	Reach	2,20	35.76	<0.001	Year	26.8
						Year × Reach	7.2
Reach [†]	Total	Reach	1,12	2.56	0.136	Year	8.2
						Year × Reach	34.9
	Native	Reach	1,12	42.08	<0.001	Year	8.5
						Year × Reach	10.3
	Non-native	Reach	1,539	149.44	<0.001	Year	37.9
Channel	Total	Channel	1,338	9.72	0.002	Year	53.7
	Native	Channel	1,338	0.10	0.753	Year	9.3
	Non-native	Channel	1,338	13.61	<0.001	Year	49.5

*Models exclude 2011 and 2012 data, but includes all reaches.

[†]Models exclude the canyon reach from all years, tests for differences between the channelised and braided reaches.

Fish assemblage variation

Reach scale. Three axes were retained from the PCA of fishes from the reach scale and explained 58.6% of the variance. The first axis explained 28.6% and was positively correlated with *C. discobolus*, *C. latipinnis* and *P. promelas* (Table 5). This axis largely reflected longitudinal variation in fish assemblages from upstream (channelised reach) with cooler water temperature and higher productivity to downstream (canyon reach, Fig. 7) with warmer water and lower productivity. The second axis explained 18.6% of the variance and was negatively correlated with *C. lutrensis*, and generally captured variation in native versus non-native fishes. The third axis explained 11.0% of the variance and was positively correlated with *I. punctatus* and *P. lucius*, summarising temporal increases in both species and spatial variation among reaches.

Indicator species analysis suggested only two species were indicators of two reaches (Table 6). Native *R. osculus* was an indicator of the channelised reach, and non-native *C. lutrensis* was an indicator of the braided reach. No species was identified as an indicator of the canyon reach.

Channel scale. Three axes were also retained from the PCA of the channel-scale data and collectively explained 54.6% of the variance. The first axis explained 26.8% of the variation and captured variation between channel types with *P. promelas* and *G. affinis* being associated with secondary channels (Table 5; Fig. 8). The second PC axis explained 16.1% of the variance and was

negatively correlated with *R. osculus*, *C. latipinnis* and *C. discobolus* and probably captured longitudinal variation in fishes. The third axis explained 11.7% of the variance and positively correlated with *I. punctatus* and negatively with *P. lucius*, potentially summarising differential habitat use by these species.

Two species were selected as indicators of secondary channels (Table 6). Both non-native *P. promelas* and *G. affinis* were in higher abundance and more frequently encountered in secondary than primary channels. No species was selected as an indicator of primary channel habitats.

Restored secondary channels

Species richness in the restored secondary channels averaged 5.3 (range = 3–8) and was lower than in the natural secondary channels in 2012 (Fig. 6). However, evenness was substantially higher in the restored secondary channels (1.2) compared to more natural secondary channels (0.75). Total, native and non-native fish densities in restored secondary channels were similar to densities found in the other secondary channels in 2012 (Fig. 6).

Discussion

Reach scale

Species richness was generally greater in the reach of the river with the most channel braiding, a pattern we attribute to greater habitat complexity. Evenness of

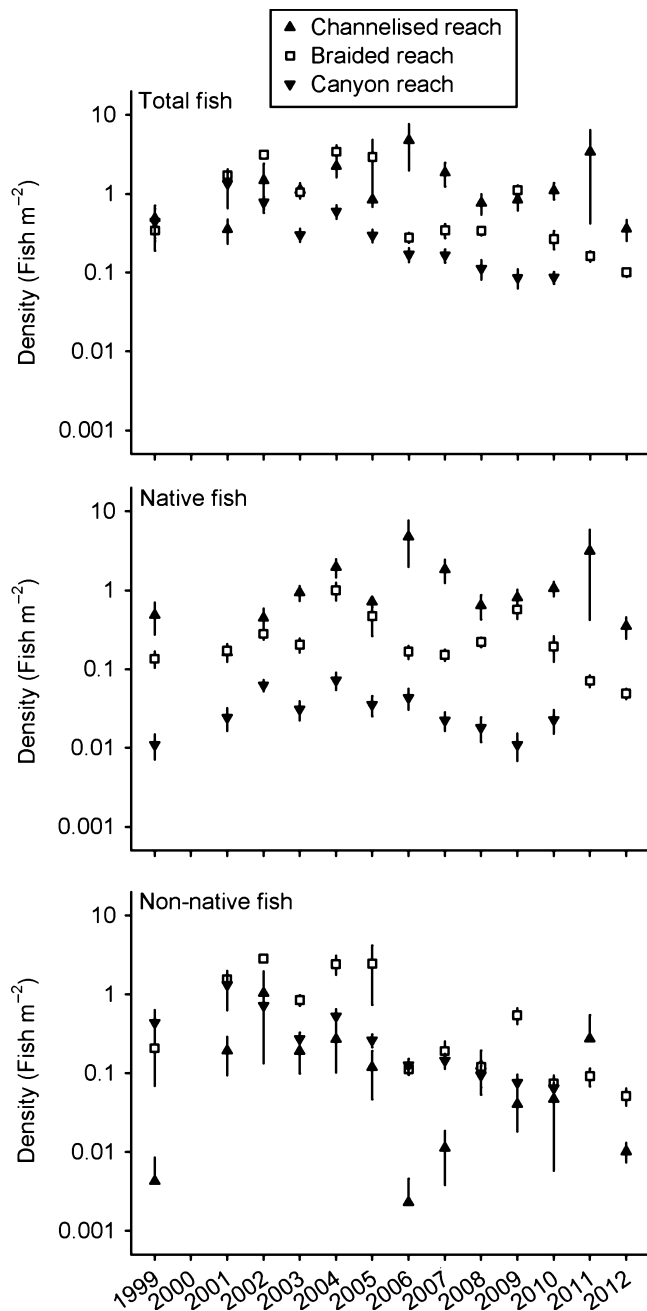


Fig. 5 Mean (± 1 SE) total, native and non-native fish densities in the primary channel by river reach during the study period.

assemblages showed little variation among reaches, suggesting most changes in fish assemblage structure were associated with their species composition. Because the native species pool is relatively small, higher species richness in the braided reach was caused by the increased incidence of non-native fishes, possibly due to increased local habitat variation (Angermeier & Winston, 1998). Because this reach-scale analysis only assessed fishes in the primary channel, stream channel braiding

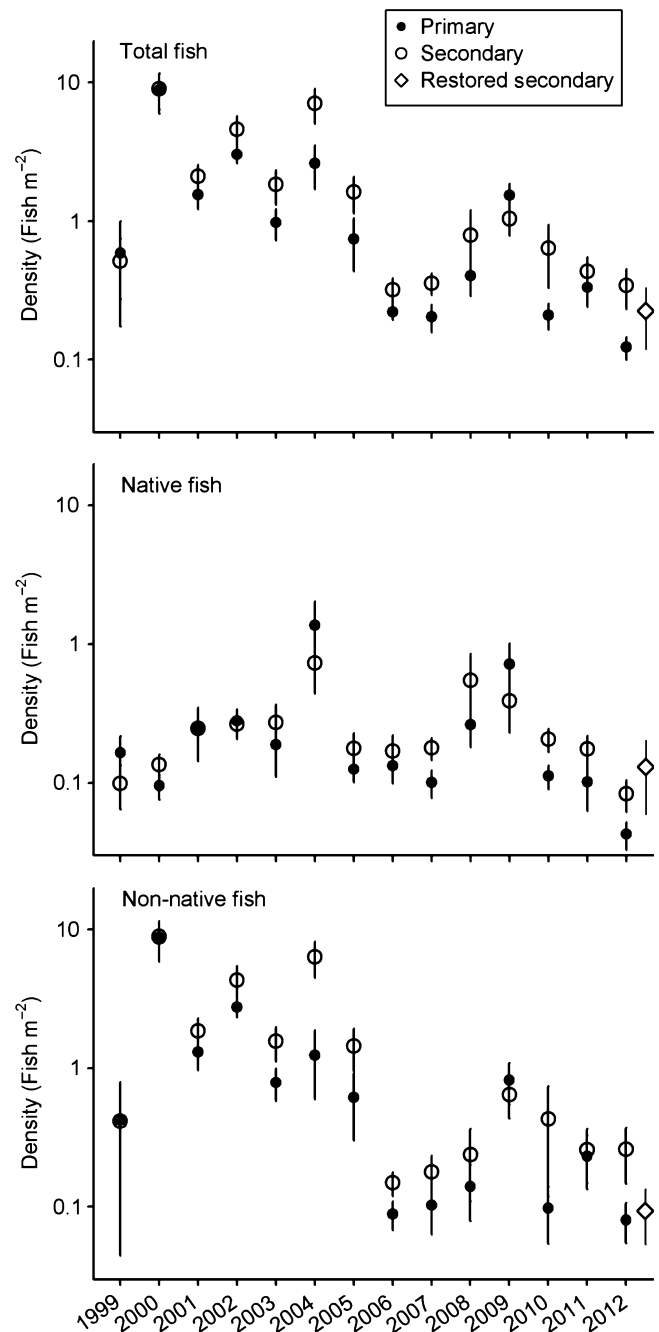


Fig. 6 Mean (± 1 SE) total, native and non-native fish densities in the primary and secondary channels in the braided reach during the study period. Fish densities in the newly restored secondary channels in 2012 are denoted.

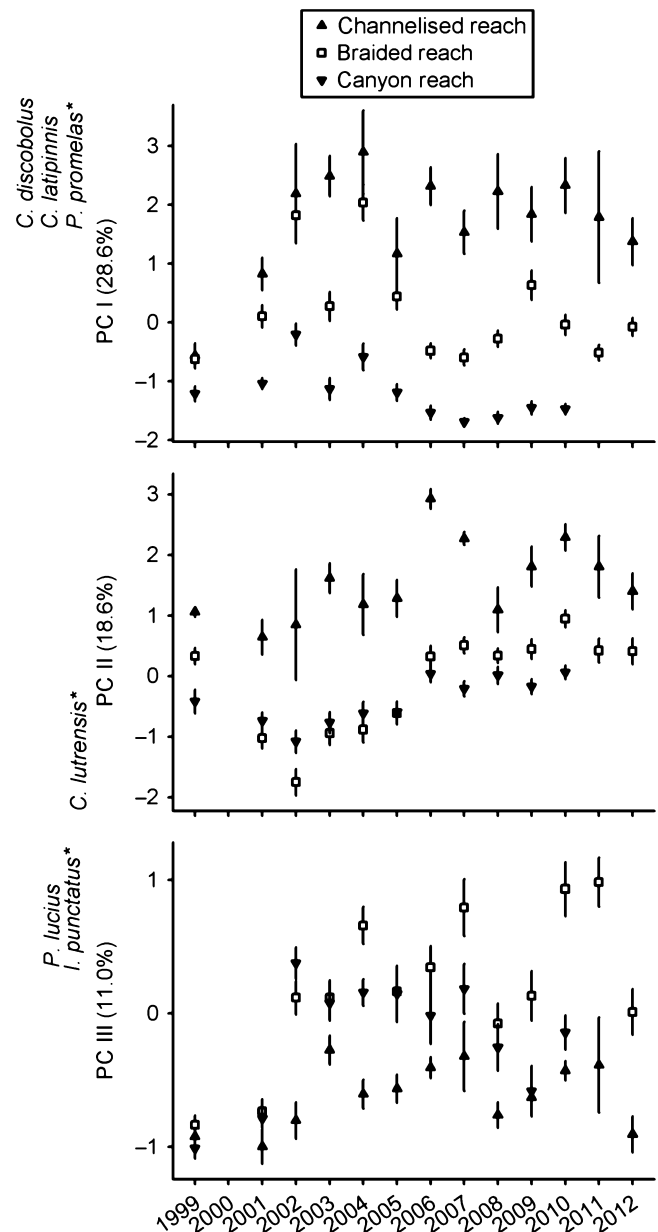
potentially facilitated non-native fish persistence at larger scales (i.e. channel braiding altered richness in the primary channel). Alternatively, the presence of secondary channels may have been correlated with other environmental variables in the primary channel that supported higher species richness. The presence of secondary channels, by definition, reduces discharge in the

Table 5 PC loadings from fish assemblages analysed at the reach and channel scale. Non-native fishes are denoted by an asterisk

Scale	Species	PC I	PC II	PC III
Reach	<i>Catostomus discobolus</i>	0.458	0.322	-0.026
	<i>Catostomus latipinnis</i>	0.457	0.236	0.188
	<i>Ptychocheilus lucius</i>	-0.033	0.210	0.728
	<i>Rhinichthys osculus</i>	0.391	0.240	0.209
	<i>Cyprinella lutrensis</i> *	0.103	-0.582	0.172
	<i>Fundulus zebrinus</i> *	0.311	-0.280	-0.083
	<i>Gambusia affinis</i> *	0.322	-0.312	-0.129
	<i>Ictalurus punctatus</i> *	-0.177	-0.320	0.579
	<i>Pimephales promelas</i> *	0.431	-0.351	0.048
	<i>Catostomus discobolus</i>	-0.264	-0.489	-0.290
Channel	<i>Catostomus latipinnis</i>	-0.248	-0.521	-0.094
	<i>Ptychocheilus lucius</i>	0.177	-0.132	-0.630
	<i>Rhinichthys osculus</i>	-0.065	-0.544	0.161
	<i>Cyprinus carpio</i> *	-0.314	0.128	0.074
	<i>Cyprinella lutrensis</i> *	-0.386	0.047	0.380
	<i>Fundulus zebrinus</i> *	-0.352	0.172	-0.213
	<i>Gambusia affinis</i> *	-0.422	0.237	-0.189
	<i>Ictalurus punctatus</i> *	0.146	-0.269	0.499
	<i>Pimephales promelas</i> *	-0.512	0.024	0.069

primary channel and potentially influences mesohabitat variation available for fishes.

Total fish densities were commonly higher in the braided reach; a pattern we suspect was driven by a higher frequency of optimal habitats for fishes. Stretches of river that were conducive to forming secondary channels probably also contain other main channel mesohabitat variability preferred by fishes (e.g. riffles, eddies) compared with more channelised reaches. A detailed assessment of the frequency of mesohabitat variability among reaches is needed to address this prediction. Conversely, primary and secondary production could also have been higher in the shallower habitats of secondary channels (Bilby & Bisson, 1992), or greater allochthonous inputs may occur with increased contact with riparian vegetation in channel braids (Kawaguchi, Taniguchi & Nakano, 2003). Nevertheless, primary and secondary production in the primary channel is generally higher in upper reaches of the river and decreases downstream (Bliesner & Lamarra, 2000). Total fish densities were lowest in the canyon reach where both autochthonous and allochthonous productivity were probably low due to limited shallow water and floodplain contact. Elevated densities of fishes, especially that of non-native fishes, in the braided reach might have occurred because secondary channels buffer populations from high flow events by providing refuge from fast water velocities (Junk *et al.*, 1989; Pearsons *et al.*, 1992; Lake, 2000; Buijse *et al.*, 2002). In the later years of our study, total fish densities peaked in the channelised reach and decreased

**Fig. 7** Mean (± 1 SE) PC scores of fish assemblages among reaches over time. Species with loadings $|>0.4|$ are denoted on the y-axis. Non-native fishes are denoted by an asterisk.

downstream. This pattern was largely a consequence of long-term declines in non-native fishes in the braided reach. Thus, it appears that density of fish was positively correlated with higher channel complexity, but this pattern was temporally variable, and largely driven by non-native fishes.

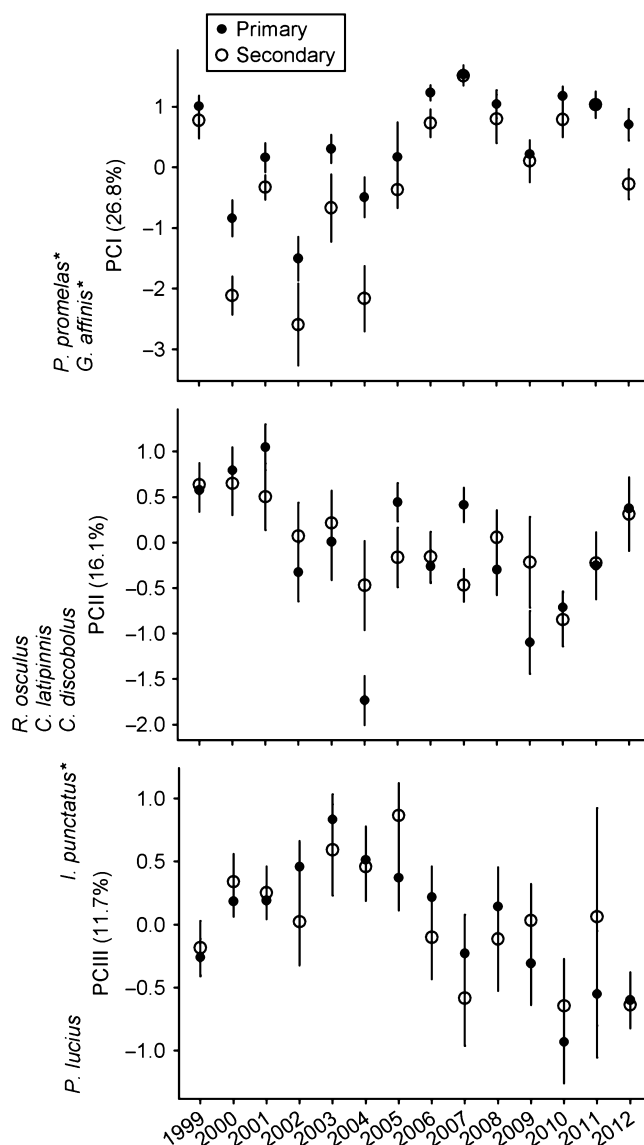
Density of the most abundant non-native fish, *C. lutrensis*, was much greater during the first half of study than the second (Supporting Material Figs. S1 and S2). Variation in the annual flow regime can differentially

Table 6 Results from indicator species analysis testing for indicator species in the different reaches and channel types. Non-native fishes are denoted by an asterisk

Scale	Group	Species	Indicator value	P
Reach	Channelised	<i>Rhinichthys osculus</i>	0.148	<0.001
	Braided	<i>Cyprinella lutrensis</i> *	0.124	<0.001
Channel	Secondary	<i>Pimephales promelas</i> *	0.08	0.001
		<i>Gambusia affinis</i> *	0.05	0.036

influence the abundance of native and non-native fishes (Brown & Ford, 2002; Kiernan, Moyle & Crain, 2012), and specifically in the San Juan River (Propst & Gido, 2004; Gido & Propst, 2012). Since 1998, managers have attempted to mimic a more natural annual flow regime characterised by elevated spring flows. Therefore, the partially managed flows may have contributed to the reduced densities of non-native fishes over time, but we cannot solely contribute their declines to the managed flow regimes given that we have not considered other potential changes in environmental conditions (e.g. habitat, climate, biotic components).

High densities of native *C. discobolus*, *C. latipinnis* and *R. osculus* higher up in the river largely drove the strong longitudinal distribution of native fishes, which contradicted our initial prediction that native fish would respond to longitudinal distribution of lateral channel complexity (Supporting Material Figs. S3 and S4). While we focused on age-0 individuals of these species, adults also have their highest densities in upstream reaches (Franssen *et al.*, 2014). In the Colorado River, these species demonstrate a similar pattern with higher densities in upstream reaches with increased riffles, higher primary and secondary production and lower amounts of fine sediment (Osmundson *et al.*, 2002). Thus, higher densities of these age-0 native fishes in the channelised reach of the San Juan River may be simply a function of the proximity and numbers of spawning adults or higher survival of larval fish in this reach due to other environmental conditions (e.g. productivity; Bliesner & Lamarra, 2000). Conversely, non-native fish densities tended to peak in the braided reach, and their densities were typically lower in the downstream canyon reach and the upstream channelised reach, suggesting these fishes were responding differently to longitudinal environmental variation. We suspect cooler water temperature (partially due to a natural longitudinal thermal gradient but also to hypolimnetic releases from Navajo Dam; Durst & Franssen, 2014) limited non-native fishes upstream and minimal habitat complexity or productivity

**Fig. 8** Mean (± 1 SE) PC scores of fish assemblages between channel types in the braided reach over time. Species with loadings $|>0.4|$ are denoted on the y-axis. Non-native fishes are denoted by an asterisk.

in the lower canyon reach limited densities there. A similar pattern of higher native fish densities upstream with lower densities of non-native fishes is also found in invaded California streams (Marchetti & Moyle, 2001).

Channel scale

Although the braided reach tended to harbour more species, species richness did not differ between primary and secondary channels, indicating non-native fishes did not exclusively use secondary channel habitats. Total fish density was greater in secondary compared with

primary channels, and non-native *G. affinis* and *P. promelas* largely drove this pattern. Although non-native fishes used the primary channel, secondary channels evidently provided conditions more conducive to supporting greater densities of non-native fishes. Several factors probably contributed to this difference. Secondary channels potentially have greater mesohabitat heterogeneity than the primary channel (Grossman *et al.*, 1998; Jackson *et al.*, 2001), have lower predation pressure or have greater resources favoured by non-native fishes than the primary channel. Both *G. affinis* and *P. promelas* often use marginal, low-velocity habitats (Pflieger, 1997), suggesting these structures may frequently occur in secondary channels. Fine-scale assessments of habitat availability and use by native and non-native fishes would lend additional insight into the proclivity for non-natives to occur in greater densities in secondary than primary channels.

The high densities of non-native fishes in secondary channels did not reduce the densities of native fishes in these habitats, suggesting limited deleterious interactions among native and non-native fishes. Similarly, the strong temporal declines in non-native fishes were not met with any striking positive response by native fishes. Some small-bodied non-native species (e.g. *C. lutrensis*) might have deleterious impacts on native fishes (Ruppert, Muth & Nesler, 1993), but the lack of compensatory responses by native fishes here suggests that densities of non-native fishes might not be limiting native fish densities. It is, however, unknown whether these non-native fishes were contributing to the apparent lack of recruitment by *P. lucius* and *X. texanus* (Farrington, Brandenburg & Platania, 2013): populations of both are still largely, if not entirely, maintained by stocking hatchery-produced individuals.

Our annual sampling each autumn did not capture seasonal variation in secondary channel habitat use by native fishes. Larval native fishes rely heavily on low-velocity secondary channels and backwaters as rearing habitats in the San Juan River earlier in the summer (Gido, Propst & Molles, 1997). As these individuals grow, especially age-0 *C. latipinnis* and *C. discobolus*, they move to the primary channel. Thus, while secondary channels may provide habitats preferentially used by non-native fishes, they also provide important rearing habitats for native fishes. Additionally, increased lateral habitat heterogeneity potentially increases the total abundance of native fishes by increasing the wetted area of the river. Therefore, higher levels of channel braiding may increase overall population sizes of native fishes that may help buffer them from perturbations

and should be considered important habitats for their persistence.

Implications for management

The loss of riverine habitat and the concurrent decline in native fishes have prompted recent efforts to restore habitat complexity in streams (Lepori *et al.*, 2005; Palmer *et al.*, 2010), and much effort and money has been expended to recreate meanders, install in-channel habitat features, and open or recreate secondary channels (Buijse *et al.*, 2002; Palmer *et al.*, 2010; Killgore *et al.*, 2012). Although it is generally acknowledged that habitat heterogeneity can facilitate coexistence of species, outcomes of river channel restoration projects on native fishes have rarely been evaluated (Bernhardt *et al.*, 2005; but see Billman *et al.*, 2013). Our results suggest construction of secondary channels in the San Juan River may increase habitat favoured by non-native fishes. Indeed, both native and non-native fishes readily colonised the newly restored secondary channels and showed generally similar assemblage structures when compared to natural secondary channels. Additionally, because fishes often demonstrate longitudinal variation in their abundances, it will be important for managers to identify areas for restoration that will have the greatest potential to benefit native fishes and minimising that for non-native fishes. Specifically, increasing channel complexity in upstream reaches of the San Juan River would be likely to aid native fishes while providing limited, or marginal, value for non-native fishes.

Our results indicate stream channel complexity can facilitate the persistence of greater species richness at different scales. While habitat complexity, in this case, tended to increase the occurrence of non-native fishes, these findings suggest channel heterogeneity may be important for retaining species diversity in riverine systems. This may be particularly true in systems with large numbers of species with a diversity of habitat preferences. However, there are surprisingly little published data on how channel braids alter the structure of available habitats and subsequently influence fish assemblages, probably due to our limited understanding of how riverine processes operate at larger scales (Fausch *et al.*, 2002).

It would be difficult, if not impossible, to experimentally assess the influence of channel heterogeneity on fishes in large rivers because of the spatial scales associated with channel braiding. However, knowing the dynamics between habitat heterogeneity and habitat use by all life stages of both native and non-native fishes is

critical to anticipating where and how management activities and restoration efforts may benefit native species or have unintended consequences by providing habitat for non-native species to flourish.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Mean (± 1 SE) non-native fish densities among river reaches from 1999 through 2012.

Figure S2. Mean (± 1 SE) non-native fish densities between channel types from the braided reach from 1999 through 2012 and in newly restored secondary channels in 2012.

Figure S3. Mean (± 1 SE) native fish densities among river reaches from 1999 through 2012.

Figure S4. Mean (± 1 SE) native fish densities between channel types from the braided reach from 1999 through 2012 and in newly restored secondary channels in 2012.

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